Contributions to the Ecology of the Cicada Killer, Sphecius speciosus *(Hymenoptera: Sphecidae)*

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ABSTRACT

The cicada killer *Sphecius speciosus* (Drury) emergence hole was linked to the wasp by a direct observation of an emergence. Wasps do not emerge via their burrows but tunnel directly from their cells to the surface. The fixed order of first emergences in the different populations appears related to the friableness of the soil. The harder the soil the later the emergence season begins. Males begin emerging before females, although there is considerable overlap. Males emerge from holes 10 mm and smaller and females emerge from holes 12 mm and larger. Holes of 11 mm are about one-half male and one-half female. The specific density or the total number of wasps over the tract inhabited by Population 1 was taken daily. The sex ratio of Population 1 was highly male biased, 2:1 based on the specific density and 3:1 based on the total number of emergence holes. *Sphecius* in the Brooklyn area apparently had no natural enemies, and wasps died of old age. The female life span is approximately 30 days and the male life span is approximately 15 days.

Studies of four populations of the solitary wasp *Sphecius speciosus* (Drury) were conducted during the summer of 1956–1963. The populations were designated 1, 2, 3, and 4, inhabiting tracts on opposite sides of 2 adjacent baseball diamonds in the Parade Grounds, a huge sandlot ball field area in Brooklyn, New York. Certain discrepancies uncovered in the literature concerning various aspects of the life history of the cicada killer are now reviewed in the light of new evidence.

Direct Observation of Emergence

The emergence hole was first described by Dambach and Good (1943) as the exit tunnel made by the young wasp in leaving the nest. It was also described as being nearly perpendicular to the surface. The emergence hole was definitely linked to the wasp in 1958, when a direct observation of emergence was made in population 1. On July 23, 1958, in the early afternoon, the surface of the ground suddenly broke in one spot, the wasp's face was visible, and after a minute's struggle the young adult was on the surface. It was inactive for 2 or 3 seconds and then flew off.

Description of the Emergence Hole

In hundreds of holes noted, nearly all were perpendicular to the surface of the ground. They are circular in shape, and the 145 holes to appear in Population 1 (1958) ranged from 6–16 mm in diameter at the surface with 10 mm being the mode diameter (N = 40). In depth they varied from 25 mm to 304 mm with more than half falling in the 76–203 mm range. The hole whose formation was observed was 88 mm deep and 10 mm in diameter.

Place of Emergence

Dambach and Good (1943) in their description of the nest found the burrow to be 30.4–45.7 cm in length from the entrance to the terminus where the first cell was excavated. A new cell was generally made immediately in front of the one just completed. As many as 4 have been found in one series. After a cell or series of cells is completely provisioned, a new lateral off the main tunnel is excavated, and the process is repeated.

Riley (1893) stated that the young wasp in leaving the nest passes through the burrow made by the female the year before. Considerable evidence to the contrary indicates that each wasp tunnels independently to the surface from its cell. The basis of this conclusion lies in the following evidence:

1. Of a total of 145 emergence holes to appear in Population 1 in 1958, all but 7 were more than 15.2 cm from a wire fence whose lower rim runs the length of the tract. Yet of the estimated 159 burrows dug in Population 1 in 1957, all but 13 had their entrance within 15.2 cm of the fence, and the bulk of these were against it. The same general picture was noticed from 1956–1963. The burrows were dug along the fence near the edge of the tract while the wasps emerged further out on the tract.

2. In Population 1 (1958) almost half of the emergence holes (44%) appeared within 3 days of another hole located not more than 35.6 cm away. Often holes appeared within centimeters of one another.

3. The emergence holes come to the surface of the ground vertically, while the burrow entrances are inclined at angles of about 45°.

4. In many years there was a much larger number of holes than of nests dug the previous year. For example, in Population 1 in 1960, there were 125 nests, yet these nests produced 939 emergence holes in 1961.

The different locations of the emergence holes and burrows are clearly expected if the wasps tunnel directly from their cells to the surface, since the cells as indicated are a distance from the entrance burrow.

The appearance of clusters of emergence holes is also to be expected if wasps from the same nest emerge about the same time from separate tunnels, and if, as according to Dambach and Good (1943), cells are made in series. The vertical emergence hole need hardly be pointed out as obviously distinct from the comparatively gently sloping entrance of the nest burrow.

Variations in the Emergence Period

In 1957 in Population 1 the date of first emergence was June 30, and the date of first emergence of Population 2 was July 1. In 1958 in Populations 1, 2, 3, and 4, the dates of first emergence were July 15, July 24, July 31, and August 7, respectively. In 1958 in Populations 1, 2, 3, and 4, the dates of last emergence were September 1, September 1, September 1, and August 14, respectively.

Seasonal fluctuations in the date of earliest emergence in a specific population can be quite large, with a difference of 23 days recorded between the first emergences in Population 2 during the years 1957 and 1958. When computed for different populations (1 and 4), a difference as great as 38 days was obtained between 2 generations (1957–1958). Climatic conditions are not entirely responsible for this fluctuation, since populations in the same field (1 and 4) under identical weather conditions can differ as much as 23 days in their date of first emergence during the same season (1958). This is hardly surprising, since a difference as great as 48 days was recorded between the first and last emergence hole to appear in a single population (Population 1, 1958). The friableness of the soil in Population 1 and its greater hardness in other populations probably explain the nearly fixed order of first emergences among the populations (see Lin 1966 and

Lin (personal communication) *in* Evans, 1966).

Dambach and Good (1943) (in computing the life span) considered the mean first date of adult life as July 1. By this they probably meant the date over a period of years which averaged the greatest number of emergences. This is apparently completely invalid for the Parade Ground populations during the summers 1957–1958, as the dates of first and last emergences show. In all cases there was only 1 emergence hole for a given population on the dates of first and of last emergence.

Emergence Time in Relation To Sex

Considerable evidence indicates that the males generally emerge earlier than the females, although there is much overlapping. As is well known, the female is usually larger than the male (Riley, 1893; Dow, 1942). Accordingly, the diameter of the emergence hole seems to provide a good index of the sex of the emerged individuals. As indicated, emergence holes varied from 6–16 mm in diameter (Population 1, 1958). It was subsequently found (1958–1967) that males emerge from holes 10 mm and smaller, and females emerge from holes 12 mm and larger. Holes of 11 mm are about one-half male and one-half female. On July 27 (Population 1, 1958) the first nest appeared. Only 1 hole which had yet appeared was as large as 12 mm, further supporting the view that holes 12 mm and larger were formed by females.

Evidence of the relationship between the size of the emergence hole and the sex of the wasp is further shown in the following account. Of a total of 66 emergence holes appearing before July 28 (Population 1, 1958), none was larger than 12 mm. On that date, 1 appeared which was 14 mm. On July 29, 2 appeared which were 13 and 14 mm, and for the first time 2 females were seen. One very huge one, by far the largest wasp seen this season, was resting on a fence railing in section 39, the same 3-m quadrat in which the 14 mm hole was located, while another very large female and a

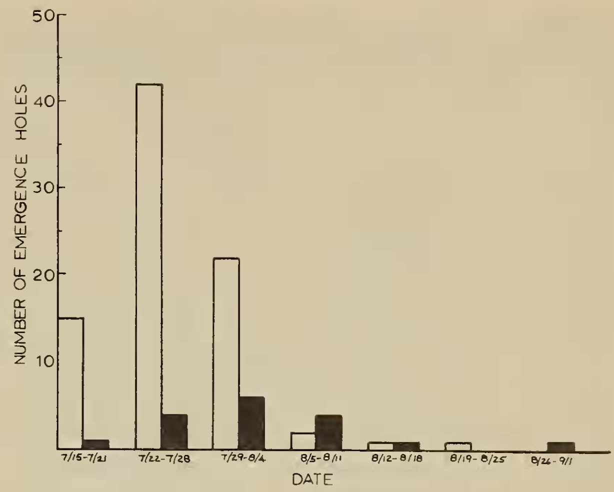

Fig. 1.—Evidence of earlier male and later female emergence is shown by the generally earlier appearance of "male" holes (clear bars) and later appearance of "female" holes (shaded bars).

male were flying around in copulo. Such a simultaneous appearance of large holes and large wasps on the same tract certainly suggests that the relationship is not fortuitous and that the appearance of large holes provides an excellent indication of the emergence of female wasps.

Fig. 1 plots the weekly total of male emergence holes against female emergence holes (Population 1, 1958) beginning on July 15, the date of first emergence. It is evident that the male holes are more common, accelerate faster, peak and decline earlier than the female holes. While the male holes are on the decline during the week beginning July 29, the female holes are in the peak stage. During the following week the decline of male holes was very sharp while the female holes were still near their peak. On July 25, 1957 (Population 1), when the emergence holes were well into the decline, 10 of the total of 14 were 12 mm or larger. What the graph does not show is the earlier appearance of the male holes. The first male hole appeared on July 15 and the first female hole on July 20. In that period before July 20, 11 male holes appeared.

Of the total 145 emergence holes to appear in Population 1 in 1958, 35 were not included in the graph for various reasons such as not having been measured because of their inaccessibility or

Table 1.—Specific density or the number of wasps present at a given time on the tract inhabitated by Population 1 in 1958. Every other date was deliberately omitted in the interests of condensing the table.

Date	Time	Specific density	Number of females	Number of males	Number unknown
7/20	0910	1	0	1	0
7/22	1803–2045	1	0	1	0
7/24	0737–0858	3	0	3	0
7/26	1520–1915	1	0	0	1
7/28	1340–1530	4	0	3	1
7/30	0821–1045	5	0	3	2
8/1	1045–1105	9	0	4	5
8/3	1045–1215	9	1[b]	3	5
8/5	0845–1008	16	1	1	14
8/7	1130–1145	9	1[a]	2	7
8/9	1355–1410	2	1[a]	1	1
8/11	1015–1050	6	2[c]	2	4
8/13	1000–1150	8	1[a]	0	8
8/15	0947–1430	7	1	3	3
8/17	1845–2020	1	1	0	0
8/19	1132	1	1	0	0
8/21	0950–1010	3	1[a]	1	2
8/23	1004–1140	3	2	0	1
8/25	1115–1130	0	0	0	0
8/27	1745–2003	3	3	0	0
8/29	1540–1700	3	3	0	0
8/31	1820	1	1	0	0
9/2	1630–1930	1	1	0	0
9/4	0800–0847	0	0	0	0
9/6	1905–1955	1	1	0	0
9/8	1040–1100	0	0	0	0
9/10	1745–1830	0	0	0	0
9/15	1820–1905	0	0	0	0

[a] = new nest or nests.
[b] = found dying.
[c] = paralyzed cicada.

having been damaged. During the first and sixth weeks only 1 11-mm hole appeared, and it was not counted as either male or female.

Daily sexing of living wasps, primarily on the basis of behavioral differences between the sexes, gives evidence in complete accord with that derived from the emergence holes. In the examination on 5 different dates (between July 30, 1958 and August 15, 1958) of the sex of wasps engaging in territorial behavior, without exception all were males (see Lin, 1963). In territorial behavior, the male defends a small area, about 2.5 m^2, against intruding males and conspicuous insects. These are chased from the area while the male continually returns to a usually localized spot (generally an emergence hole) within the territory. Territorial behavior thus becomes a means for recognizing the male. The female is likewise recognized by behavior such as the manner of flight, leaving or entering the nest, digging, or carrying a cicada to the nest.

Specific Density

Table 1 contains an exact, or nearly exact, determination of the specific density (total number of wasps over or on the tract inhabitated by Population 1, 1958) at any one point during the time listed. The specific density was determined by total counts repeated several times after which the same sum was usually obtained. It is the large size of the wasp and its tendency for localization, whether the male around his territory or the female around her nest, which makes this most accurate of methods possible. On some occasions when the number of wasps was greatest, the highest count with certainty that no wasp had been counted twice was taken as the density. The vertical bars on the fence broke the tract up into 51 3-m sections for a total of 153 m.

During most determinations of the specific density, a number of wasps completely at random (dependent on chance opportunity) were sexed, usually by behavioral determinations; sometimes by anatomical means consisting of body segment counts while in the field. As Table 1 shows, in complete agreement with the evidence from the emergence holes, the males appeared earlier, peaked earlier and declined earlier than the females. In Population 1 (1957) the first male was recorded on July 3 and the last on July 25. The first female was recorded on July 14 and the last on Aug. 27. In Population 3 (1958) the first male was recorded on Aug. 4 and the last on Aug. 23. The first female was recorded on Aug. 9 and the last on Sept. 3. Fig. 2, based upon data from Table 1 (including the data omitted to condense the table), with the exclusion of indirect signs, shows the weekly sex ratio for Population 1 in 1958. It is readily seen that numbers of males are on the decline before the females reach their peak. The males then disappear entirely while the females are still present. This graph bears a striking resemblance in the relative number of males to females for any week to that of the relative number of male to female emergence holes the week before, as shown in Fig. 1. In later years it was found that the females rejoin the society about a week after emergence, and males spend considerably more time in their territories after about a week after emergence. During the week July 15–21, only male emergence holes appeared, with one exception. In the week beginning July 20 only males were observed. In the week of July 22–28 there was an increase of female and male holes and in the following week the number of females relative to males was about what might be anticipated from the emergence holes. To give a final instance, in the week of August 5–11, the male holes had greatly declined so that the numbers of male holes and female holes were almost equal. The situation was almost the same for the relative numbers of males and females for the following week. This similarity between the graphs has a basis if males emerge predominately from holes 10 mm and smaller while females emerge from those which are 12 mm and larger. This similarity is also based on the extensive marking data of later years showing that wasps habitat imprint to the tract from which they emerged. The inevitable conclusion is that females were seen later in the season because they generally emerged later. Also, as will be shown, the female life span is approximately double the male life span.

The Sex Ratio

Dambach and Good (1943) in their review of the sex ratio gave the following account. "Of 25 adults emerging from stored larval cases, 15 were males and 10 were females. Seven collected in Muskhigum County were females, and of specimens at Ohio State University and Ohio State Museum, 29 were males and 37 were females. Denton (1931) obtained 13 females and 7 males from a group of 20 he collected from a colony on August 2, 1930 at Robbinville, North Carolina. These collections totaling 128 specimens indicate a sex ratio of 70 females to 48 males or 59.3% females to 40.7% males." Only their data obtained from stored larval cases can be considered reliable. Dow (1942) likewise obtained a male biased ratio from adults (6 females and 12 males) reared from 18 stored cocoons he collected.

Dambach and Good's (1943) method in determining the sex ratio is invalidated by their method of adding together the total males and females caught by different observers from completely unrelated populations. They failed to take into consideration such factors as the differ-

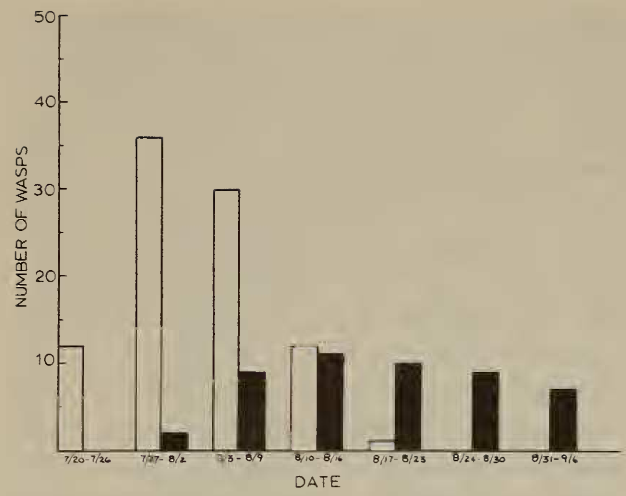

Fig. 2.—The weekly sex ratio (males clear bars, females shaded bars) based only upon the number of wasps sexed in determinations of the specific density, shows considerable fluctuation. Absolute numbers between any 2 weeks should not be compared, since more determinations of specific density were made in some weeks than in others.

ences in the time of emergence between the sexes, the longer active season of females, and the tendency of females to be present on the tracts the entire day, while the males seldom remain past the morning. To illustrate the former, if, as shown in Fig. 2 using Dambach and Good's method, collecting was done in Population 1 between July 20 and July 26, the conclusion arrived at would be a population of 100% males. Conversely, if collections were made between August 24 and September 6, the conclusion would be a population consisting of 100% females.

Lin and Michener (1972) state, "it seems that the evolution of the sex ratio depends more on the natural history of the species" in reference to male haploidy. According to White (1954) the entire order of Hymenoptera with the exception of a few species show haploid parthenogenesis. White states, "It is characteristic of groups with haploid males that the sex ratio fluctuates rather widely from species to species and from strain to strain within the species, and also to some extent with various environmental factors, showing no particular tendency to conform to any fixed percentage of males". Consequently the sex ratio becomes meaningful only in terms of the population and even here seasonal fluctuations are likely to be considerable, so that separate determinations should be made for each season.

In Population 1 (1958), 139 wasps were sexed during daily determinations of the specific density. A total of 121 wasps were not sexed although their behavior strongly suggested males. Only the wasps themselves, living or dead, were used in determining the sex ratio, since indirect evidence like new nests or paralyzed cicadas would obviously distort the picture in favor of the female. Fig. 2 plots the weekly sex ratio, which is seen to vary considerably. By taking the sum total for all the weeks of the season, a seasonal ratio of 91 adult males to 48 adult females (65% males to 35% females) in the Population 1 area (1958) is obtained. The high male frequency suggests possibly the easier recognition of the male behaviorly rather than so great a number of males. This possibility has been considered, and it appears that this conclusion would be unwarranted.

Of the 110 emergence holes Fig. 1 (Population 1, 1958) the ratio of male holes to female holes was 83 to 27 or 3:1. In 1959 the ratio was 132 to 22 or 6:1, in 1960, 137 to 45 or 3:1; in 1961, 630 to 212 or 3:1; in 1962, 596 to 235 or 2.5:1; and in 1963, 93 to 53 or 1.7:1.

Adult Longevity and Mortality

Dambach and Good (1943) consider July 1 and September 1 as the mean first and last dates of adult life and thus approximate the life span of the adult to be 65 days.

In 1956–58 dead and dying wasps were found on the tracts between August 3 and 31. The dead wasps were in most cases in perfect condition. Though wasps were usually present in considerable numbers before August, out of a total of 20 dead or dying, none was found in July. There was in these cases no evidence of predation though on the other hand the good condition of the dead wasps, the wasps found dying from no apparent outside

Table 2.—Adult *S. speciosus* longevity table.

Year	Location	First emergence hole	Dead wasp found	Sex	Maximum age of wasp (for population)
1957	Population 1	6/30	8/4	♀	35 days
1957	Population 1	6/30	8/7	?	38 days
1957	Population 1	6/30	8/8	♀	39 days
1957	Population 1	6/30	8/9	♀	40 days
1957	Population 1	6/30	8/14	♀	45 days
1958	Population 1	7/15	8/3	♀[a]	19 days
1958	Population 1	7/15	8/10	♂	26 days
1958	Population 3	7/31	8/11	♂[a]	11 days
1958	Population 3	7/31	8/12	♂	12 days
1958	Population 3	7/31	8/13	♂	13 days
1958	Population 3	7/31	8/14	?	14 days
1958	Population 1	7/15	8/16	♀	32 days
1958	Population 1	7/15	8/18	♀	34 days
1958	Population 1	7/15	8/19	?	35 days
1958	Population 4	8/7	8/19	?	12 days
1958	Population 1	7/15	8/20	♀	36 days
1958	Population 3	7/31	8/23	?	23 days
1958	Population 1	7/15	8/23	?	39 days
1958	Population 3	7/31	8/24	?	24 days
1958	Population 2	7/24	8/31	♀	38 days

[a] found dying.

causes, and the period in which dead wasps were found, make it highly improbable that death (at least in most cases) was due to anything other than old age. No natural predators of the adult cicada killer have been observed in Brooklyn during the period of study.

In 1957 the first emergence hole on the tract inhabitated by Population 1 appeared June 30. The last dead wasp on this tract was found on August 14, thus no wasp was older than 45 days. In 1958, the first emergence hole on the tract inhabited by Populations 1, 2, 3, and 4 appeared respectively July 15, 24, 31, and August 7. Table 2 gives the maximum age of wasps found on each tract.

In 1958 in Populations 1–4, 32% or more of the emergences took place on or after August 1. It is these later emergences which probably account for wasps seen in late August or September. Dambach and Good (1943) were probably unaware of these later emergences (since marking the emergence holes appears necessary), and attributed all wasps of the season to emergences in early July.

Table 2 reveals a pattern with 3 exceptions in which the maximum age of females dying were in their 30's. Males of which there were only 4 with 1 exception of 26 days, were 11, 12 and 13 days of age. In later years, a number of males and females were captured and marked on emergence and followed daily for their entire lives. This highly precise data indicates that Table 2 is roughly correct. Males live about a maximum of 15 days and females live a maximum of about 30–33 days.

Acknowledgments

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Colaspis quattuordecimcostata *Lefèvre and Its Close Relatives in Brazil*

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ABSTRACT

Colaspis quattuordecimcostata Lefèvre is redescribed from the type specimen, and nine additional Brazilian species of *Colaspis* are described and figured.

In my studies of the Chrysomelidae I have had difficulty in establishing the true identity of the species from Brazil described by Lefèvre in 1887 as *Colaspis quattuordecimcostata*. My study of Lefèvre's type was made possible by Nicole Berti, who sent the holotype from the Natural History Museum in Paris for my examination. There are 9 closely related new species of *Colaspis*, all from Brazil, which I am describing in this paper.

Colaspis quattuordecimcostata Lefèvre

(Fig. 1)

Colaspis 14-costata Lefèvre, 1887. Ann. Soc. Ent. France, 1887, p. 144–45.

Length 11 mm. Width 4.3 mm.

Oblong oval, shining black with mostly black antennae.

Head black with fine punctures, interocular space half width of head, a medium depression down front, labrum dark brown, antennae with only joints 2 and 3 pale. Prothorax twice as broad as long, margin with tooth below middle, disc with moderately dense punctures. Scutellum shining black. Elytra a little more than 3 times as long as prothorax and wider, punctures in geminate rows except near suture where in single row and near the apex of second row, with well marked costae. Body beneath with blue-green lustre. Legs black, hind tibiae short and almost the same length as other tibiae.

Holotype.—Female, Natural History Museum, Paris (from which I borrowed the type specimen and made a drawing).

Type-locality.—Brazil.

Remarks.—The most striking character in this species is the very short hind tibiae.

Colaspis paracostata, n. sp.

(Fig. 2)

Length 8 mm. Width 4 mm.

Elongate oblong oval, shining black with dark blue-black head and prothorax.

Head with dense fine punctures, labrum brown. Interocular space a little more than half width of head, antennae with only third joint pale. Prothorax approximately twice as wide as long, margin with tooth below middle, disc sparsely punctate. Elytra more than 3 times as long as prothorax